

Taxonomy and distribution of the boreomontane shore bugs *Salda sahlbergi* and *S. henschii* (Heteroptera, Saldidae)

PER LINDSKOG

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Additional taxonomic characters are given and illustrated supporting the concept of *Salda sahlbergi* Reuter and *S. henschii* (Reuter) as separate species. Their present assignment to the genus *Salda* (s. str.) is shown to be poorly substantiated. Salient characters of the male genitalia suggest that they may be more closely related to *Teloleuca*. *S. henschii*, hitherto only known from the mountains of Central Europe, is recorded for the first time from Sweden and Eastern Fennoscandia (USSR) in northern Europe. It is here confined to freshwater wetlands in lowland coastal areas within the subboreal (boreo-nemoral) zone. Revised data on the geographic distribution of *S. henschii* and its boreal sister-species, *S. sahlbergi*, are summarized. The latter is for the first time reported from the New World (Canada, Newfoundland). Data on habitat and life cycles are given. The biogeography of this species pair is discussed in some detail with respect to vicariance relationships, range disjunctions, and local historic-ecological phenomena reflected in their Fennoscandian distributions. The former issue is centred on the nature and interactions of the Angaran and European areas of endemism, the latter on the significance of isostatic land uplift.

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Introduction

The *Salda* group of shore bugs includes 21 species in three genera: *Salda* L. (Holarctic), 16 spp.; *Teloleuca* Reuter (Holarctic), 4 spp.; and *Lampracanthia* Reuter (Nearctic), 1 sp. (cf. Schuh et al. 1987). They form a strictly Holarctic-boreal and temperate group, the species appearing as characteristic elements of the saldid fauna of the Northern Coniferous (Taiga) zone and corresponding mid-latitude montane life-zones in the Old and New World. Most species are comparatively large, ca 5–7 mm, predominantly dark coloured, and exhibiting alary polymorphism, with a prevalence for flightless (semibrachypterous) morphs. *Salda* and *Lampracanthia* primarily inhabit fresh water marshes, bogs, and damp meadows, including alpine sites, in a few cases also saline formations. The *Teloleuca* species are primarily associated with the open sandy-stony banks of streams and rivers, partly [*T. pellucens* (F.)] also occupying more terrestrial habitats, as moorlands and alpine heaths, or sparsely vegetated ground and decaying mossy logs in montane and boreal coniferous forests (e.g. Schuh 1967, Brooks & Kelton 1967, Wróblewski 1966, Lindskog 1975, Cobben 1985).

Among the nine *Salda* species recorded from the Palearctic, *S. sahlbergi* Reuter and *S. henschii* (Reuter) are somewhat isolated with respect to various taxonomic characters. These two species were earlier placed in the genus *Saldula* until correctly transferred to the *Salda* group (Saldini) by Cobben (1959, 1960), primarily on the basis of unmistakably synapomorphic characters of the male genitalia. Drake & Hoberlandt (1951) synonymized *S. henschii* (= *Saldula umbrata* Schmidt) with *S. sahlbergi*, a view also followed by Cobben (1959, 1960). More recently Hoberlandt (1977) restored *S. henschii* as a separate species.

According to present knowledge (Hoberlandt 1977, Schuh et al. 1987, Péricart 1990) *S. henschii* would be restricted to the mountains of Central Europe (mainly the Alps and the Carpathians), as opposed to *S. sahlbergi* being a true boreal species ranging from Scandinavia to the Soviet Far East.

However, I have now confirmed the presence of *S. henschii* in northern Europe (Fennoscandia), and revised various materials identified as *S. sahlbergi* from northern Europe and Asia. The new data on the distribution of these species are given here, including the first record of *S. sahlbergi* from the New World. As a supplement to the study by Hoberlandt (1977), who separated *sahlbergi* and *henschii* mainly on differences in hemelytral colouration and dorsal pilosity, I present additional and more detailed data on discriminatory characters of these species. Special attention is paid to some biogeographical patterns pertaining to this species pair.

New important data on the taxonomy and distribution of the Eurasian species of the *Salda* group were recently provided by the late Dr René H. Cobben (Cobben 1985). He deliberately refrained from considering the present two species in his paper, instead referring to my study for further details (cf. Cobben 1985:262, foot-note).

Material and methods

Material has been studied from the following collections (abbreviations in parenthesis): Naturhistoriska Riksmuseet, Stockholm, Sweden (NRS); Entomologiska Museet, Lunds Universitet, Lund, Sweden (EML); Zoologisk Museum, Oslo, Norway (ZMO); Universitetets Zoologiska Museum, Helsinki, Finland (ZMH); Zoologicheskii Institut, AN SSSR, Leningrad, U.S.S.R. (ZIL); Laboratorium voor Entomologie van de Landbouwhogeschool, Wageningen, the Netherlands (WAG); Department of Biology, Nankai University, Tianjin, Peoples Republic of China (NUT).

In addition to the new material from Northern Europe listed further below, *S. henschii* was also studied from Austria: Nordtirol, Seefeld, Wildmoosalm, ca 1 300 m, 5♂7♀, partly reared from larvae (L5), 1.vii.1973, P. Lindskog (NRS); Kärnten, Weissensee, 30.vii.1958, 4♂2♀, H.-H. Weber (NRS).

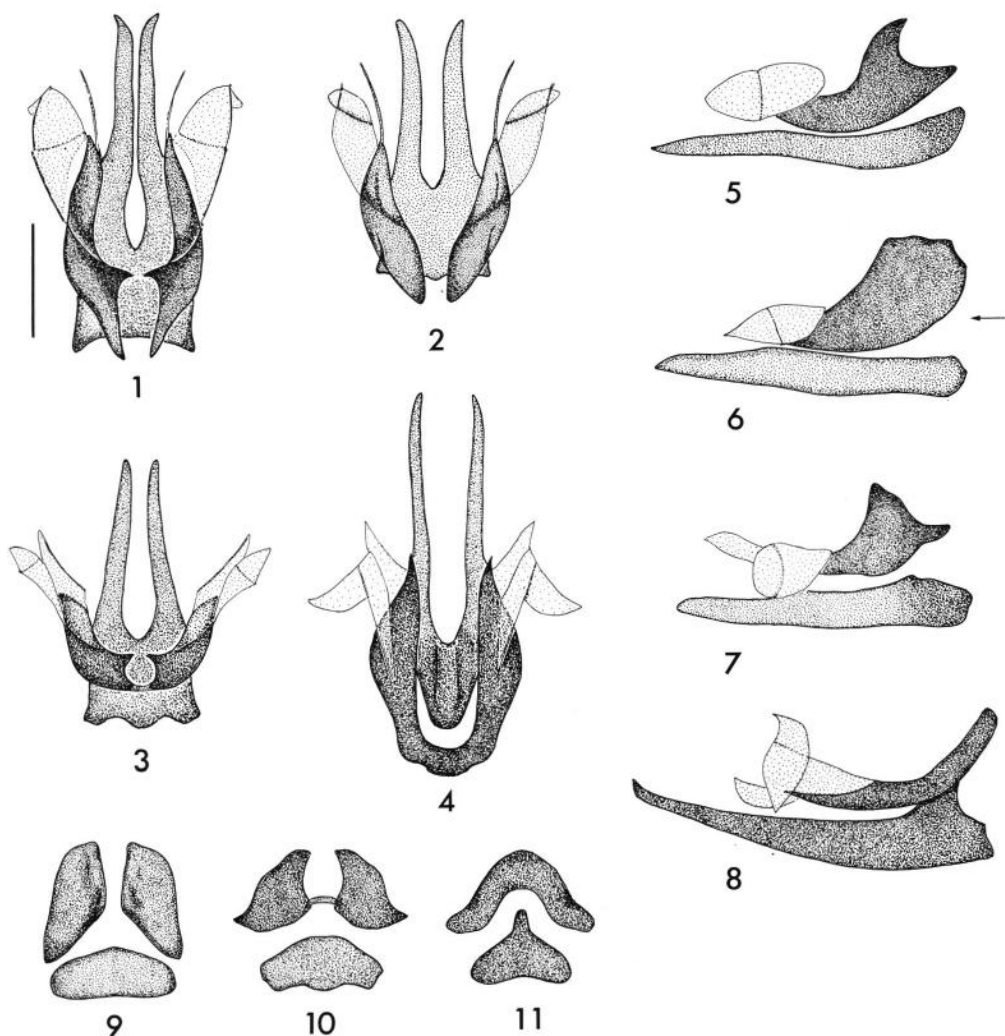
Eunomies of hemelytral pigmentation are attributed a decisive role as characters in the differentiation of species in saldid taxonomy (e.g. Cobben 1960). There is an obvious need, both at taxonomic and evolutionary studies of the group, for developing a more strict basis for the comparative analysis of saldid wing patterns. Accordingly, it is clear that the various components of these

patterns, including centers of melanization and spread of dark pigmentation, have definite relationships to and are compartmentalized by wing topography, primarily the corial veins and the cells enclosed by them. As a first step in establishing a nomenclature for identifying these components, I provide a figure with names for the cells in the saldid corium (Fig. 32). I essentially follow the practice in naming insect wing cells according to the identity of the anterior vein enclosing them. The identification of veins follows Polhemus (1985) and Wotton & Betts (1986). This permits a topographic definition of components of saldid wing patterns by referring to the "radial spot", "median eye spot", "basicoastal centre of melanization", etc. One should note that the preradial vein identifiable as subcosta is only more exceptionally plainly visible or completely developed in the Saldidae. Generally, the course of Sc and thus the border between the costal and subcostal cells or fields (the two terms being used interchangeably here), is indicated as a more or less clearly defined depression of exocorium delimiting the reflexed costal margin (cf. Fig. 32, stippled line), most evident in the proximal part of exocorium. This typically corresponds to a demarcation line between a different surface texture (e.g. costal field shiny /subcostal field dull) or pigmentation of exocorium. The latter pattern is especially apparent in the eunomy of species like *Saldula opacula* (Zetterstedt) and others, where dark pigment spreads along this line and then gradually expands inwards over the subcostal field, leaving a continuous and neatly delimited, light costal stripe (e.g. Cobben 1960:figs 142-149).

Taxonomy

Relationships of the *sahlbergi* group

The present paper is an off-shoot of my still ongoing revision of supraspecific relationships in the *Salda*-group and studies of the relationships between this group and other saldine taxa. Suffice it to note here that the current assignment of the *Salda*-group to a separate tribe, Saldini, which would form the sister group of Saldoidini (=Charotscirtini of Cobben) (Cobben 1959, Polhemus 1985), is poorly substantiated by cladistic data at hand. The Saldoidini encompasses all remaining saldine genera minus *Salduncula* (Saldunculini)



Figs 1-11. *Salda* group, male endosomal sclerites. — 1-4. Frontal view. — 5-8. Lateral view; arrow directed anteriorly. — 9-11. Basal view. — 1, 5. *Salda sahlbergi* Reuter. — 2, 6, 9. *S. henschii* (Reuter). — 3, 7, 10. *Teloleuca pellucens* (F.). — 4, 8, 11. *T. bifasciata* (Thomson). Scale line 0.1 mm.

Hanens endosomal skleriter. — 1-4. Framifrån. — 5-8. Från sidan; pilen pekar framåt. — 9-11. Från basen.

according to the most recent higher classification of the Saldidae (Polhemus 1985). Instead, as will be demonstrated elsewhere, the Saldini is probably more closely related to some subgroup of Saldoidini, the latter thus standing out as paraphyletic (Lindskog & Chen, in prep.).

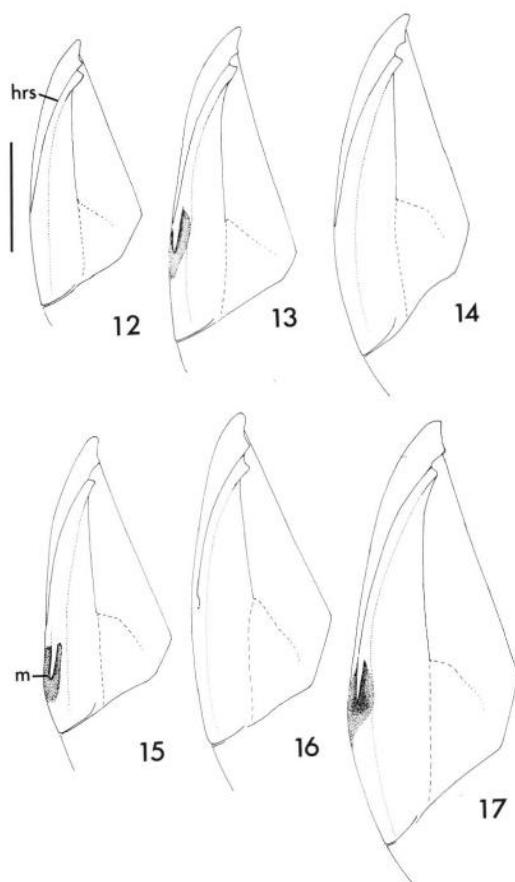
One further point concerns the actual delineation of the three genera of the *Salda* group. [The question of their rank, i.e. either classifying them as subgenera of the single genus *Salda* (Cobben

1959, 1960), or upholding their status as separate genera (Polhemus 1985, Schuh et al. 1987), is of secondary concern here.] I have earlier noted that *S. henschii* (Lindskog 1975:166, as a form of *sahlbergi*) more agrees with *Teloleuca* than with *Salda* with respect to the structure of the male endosomal (phallic) sclerites. The same applies to *S. sahlbergi*. Unlike all other Old or New World *Salda* species the upper sclerotized pieces of the complex median sclerite are not united basally

with the inner furciform sclerite in *sahlbergi*+*henschii*, a condition shared with *Teloleuca* (see Figs 1, 2, 9) and *Lampracanthia*. (The presence of an inner furciform sclerite is a synapomorphy of the *Salda* group.) Further and most importantly, the upper pieces are not connected basally in *sahlbergi*+*henschii*, i.e. not forming a single U- or V-shaped sclerite as in other members of the group together with all remaining Saldinae (Figs 1, 2). However, in *T. pellucens* the basal connection is incomplete, only consisting of a narrow ligamentous strand (Figs 3, 10). Excepting the latter structure, the endosomal sclerite of *T. pellucens* closely agrees with the former two species. In the other *Teloleuca* species the two pieces are broadly and solidly united (Figs 4, 11; see also Cobben 1985: fig. 20d).

Polhemus (1985) differentiated and diagnosed *Salda* and *Teloleuca* by characters of the hypocostal region of the hemelytron. In *Teloleuca* the secondary hypocostal ridge (hrs) joins the costal margin in a shallow V (Figs 14, 15); in *Salda* the distal end of hrs does not meet nor point at the costal margin (Figs 16, 17). I have confirmed the validity of these observations, though with two notable exceptions: the hrs of *S. sahlbergi* and *S. henschii* agree with *Teloleuca*, not with *Salda* (Figs 12, 13). *Lampracanthia* conforms to *Salda* in this character, disregarding a deviant, true laminar structure of the hypocostal ridge (hr) in the former. Further, contrary to the statement by Polhemus (1985), the hypocostal ridge is distally modified to facilitate coupling with the male abdominal grasping apparatus not only in females of all typical *Salda* spp. (as well as *S. henschii* and *S. sahlbergi*) but also in all *Teloleuca* species, except *T. pellucens*, which has an unmodified coupling region (cf. Figs 12–17). The latter state is shared with *Lampracanthia*.

The phylogenetic meaning of these conflicting patterns in character states and the present generic assignment of *S. sahlbergi* and *S. henschii* are not yet clear. The similarity between *Teloleuca* and *sahlbergi*+*henschii* in the structure of hrs is most readily interpreted as a symplesiomorphy (as judged by out-group comparisons), hence not providing evidence for a closer relationship. The similar structure of the median phallic sclerite in *sahlbergi*+*henschii* and *Teloleuca* (primarily *T. pellucens*, the type species of the genus) is more problematical. It may be another symplesiomorphy, i.e. represent the ancestral condition in



Figs 12–17. *Salda* group, right fore wing, ventral view, with details of hypocostal margin. — 12–13. *Salda henschii* (Reuter). — 12. ♂. — 13. ♀. — 14. *Teloleuca pellucens* (F.), ♀. — 15. *T. brancziki* (Reuter), ♀. — 16–17. *Salda littoralis* (L.). — 16. ♂. — 17. ♀. Abbreviations: hrs = secondary hypocostal ridge; m = area of female hypocostal ridge modified for coupling with male abdominal grasping apparatus. Scale line 1 mm.

Höger framvinge underifrån med detaljer av den hypocostala kanten.

the *Salda*-group which is retained in these taxa. Alternatively, it is an apomorphy defining a clade comprising *Teloleuca* (s.str.) and *sahlbergi*+*henschii*. This latter alternative would seem more likely in view of the uniqueness of this character state. In either case, *S. sahlbergi* and *S. henschii* clearly fall outside typical *Salda* (plus *Lampracanthia*) in these and additional characters not treated here. No decisive evidence is available supporting the current concept that *sahlbergi*+*henschii* are more closely related to *Salda* than

Tab. 1. Differential characters of *Salda sahlbergi* Reuter and *S. henschii* (Reuter).

Character	<i>S. sahlbergi</i>	<i>S. henschii</i>
General colour	Dullish brown	Moderately shiny black
Light radial spot on endocorium	Undivided, crescent-shaped, also in darkest forms (Figs 20–22)	Reduced, only its proximal and/or distal end persisting as small roundish spots (Figs 23–25)
Acetabula	Margined with light brownish-testaceous	Entirely black
Dorsal pubescence	Uniformly short, recumbent	Moderately long, semi-recumbent, partly suberect
Parandria	Slender, tapered, mesal margins subparallel, proximally broadly separated (Fig. 26)	Broad, blunt, mesal margins distally diverging, proximally narrowly separated (Fig. 27)
Parameres	See Fig. 28	See Fig. 29
Upper pieces of median endosomal sclerite	Basally indented, bicuspidate in lateral view (Figs 1, 5)	Basally irregularly rounded, club-shaped in lateral view (Figs 2, 6)
Apex of second ovipositor gonapophysis	Without small subapical tooth (Fig. 31)	With small subapical tooth (Fig. 30)

to *Teloleuca*. These sister species should be referred to as the *sahlbergi* species group, whose relationships to other *Salda* group taxa remain uncertain.

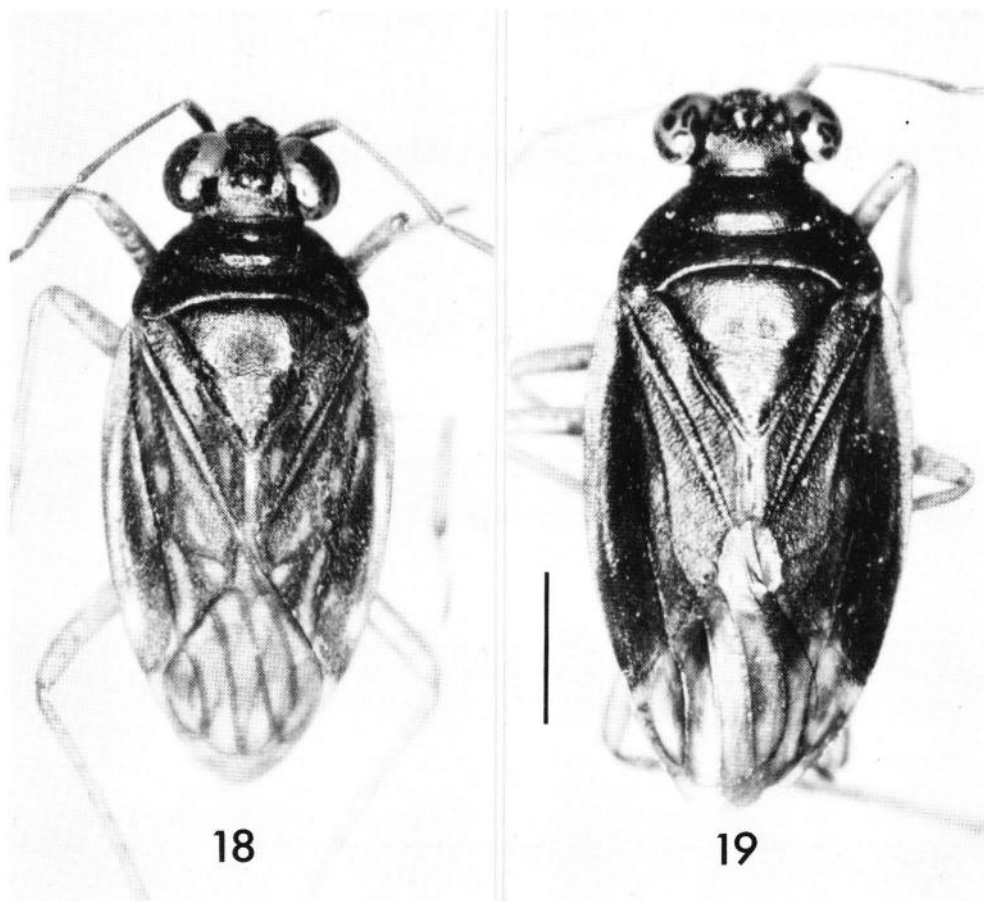
In general appearance *S. sahlbergi* and *S. henschii* look more similar to certain species of the genus *Macrosaldula* than to other species of the *Salda* group (Figs 18, 19). While a confusion with the North and Central European *M. scotica* (Curtis) and *M. variabilis* (H.-S.) is unlikely, some of the numerous Asian representatives of this genus of monticolous riverine and lapidicolous shore bugs converge rather closely in external facies to the *sahlbergi* group [e.g. *M. jakovleffi* (Reuter) and *M. nivalis* (Lindberg)]. In addition to the differences in male genital structures (e.g. Cobben 1985), members of *Macrosaldula* may be separated from the *Salda* group by their lack of a secondary hypocostal ridge. Only *M. rivularia* (J. Sahlberg) and *M. koreana* (Kiritschenko) belonging to a small subgroup [together with *M. monae* (Drake) and *M. simulans* Cobben], which deviates in several characters from typical *Macrosaldula*, possess such a ridge (only present by its proximal end in *monae* and *simulans*) (Lindskog unpubl.).

Species differentiation

The differences in somatic and genital characters (Tab. 1) clearly support the concept of *S. henschii*

as a distinct species, hence fully confirming Hoberlandt's (1977) conclusions. Generally, the colour pattern combined with the longer and more erect dorsal vestiture of *henschii*, rendering this species a clearly hirsute appearance, suffice for a reliable separation from *sahlbergi*.

S. henschii was earlier regarded as merely representing darker colour forms of *sahlbergi* (cf. Cobben 1960: figs 47–48 = *sahlbergi*, fig. 49 = *henschii*). While *henschii* is generally darker with more reduced light hemelytral markings, differences nonetheless exist between the two species in details of the eunomic (serially directed) pattern of variation in the light and dark colouration of the hemelytra (Figs 20–25). Some clear incongruities in the pigmentation eunomies of *S. henschii* and *S. sahlbergi* may be defined. Most characteristic, the elongate light radial spot in the distilateral corner of endocorium persists through all phases of the darkening eunomic series in *sahlbergi*. It only adopts a more narrow crescent-like shape as a result of progressive spread of dark pigmentation out from the zone of the bordering veins (R and M) (Figs 20–22). Conversely, the lightest colour phases of *henschii* (Fig. 23) have the radial spot largely obliterated by dark pigment, only persisting as two small dots representing its anterior and posterior end. Significantly, the specimen depicted in Fig. 23 may be regarded as representing a more light phase in the eunomic



Figs 18–19. *Salda*, male habitus. — 18. *S. sahlbergi* Reuter, U.S.S.R.: Karelia, Jaakimavaara, leg. J. Sahlberg. — 19. *S. henschii* (Reuter), Sweden: Uppland, Runmarö, leg. C. Hoffstein.

Hane uppifrån.

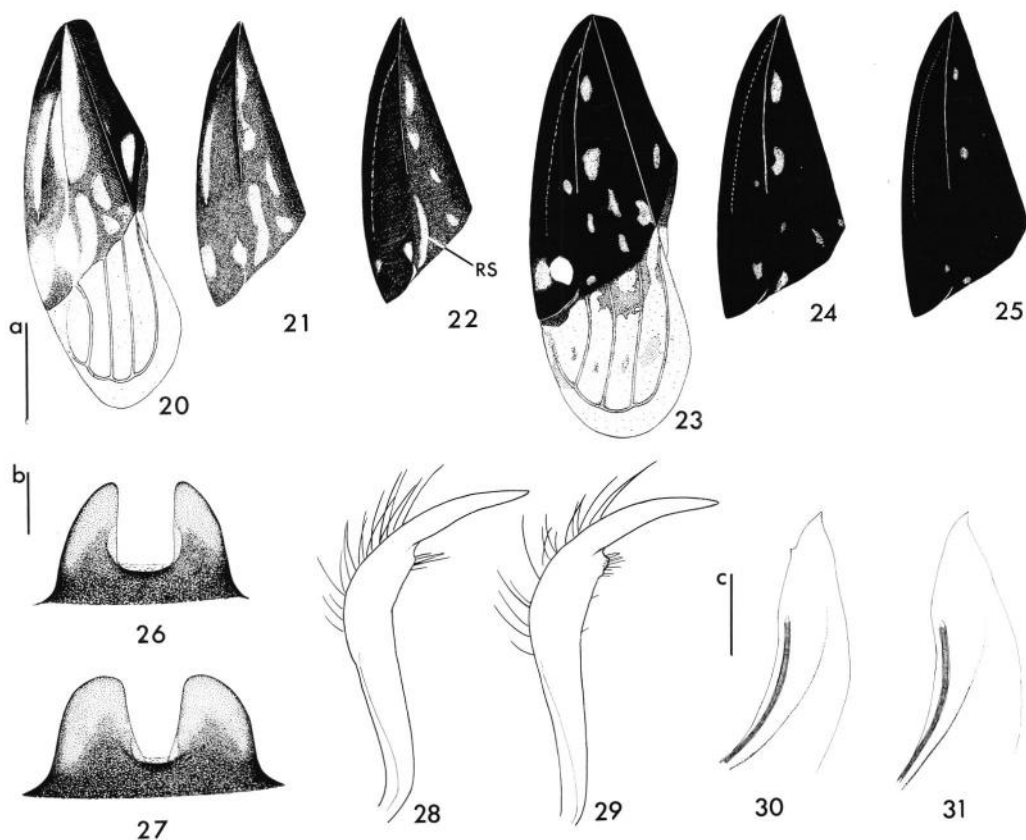
series than the dark form of *sahlbergi* with continuous radial spot shown in Fig. 22, at least with respect to the stage of darkening of exocorium. Accordingly, in the *henschii* specimen the two light subapical spots of exocorium, comprising an outer costal and an inner subcostal spot, are comparatively large and still only narrowly and incompletely separated by dark pigment spreading forward along the Sc vein from a distal centre of melanization bordering the costal fracture. In addition a small light spot is present centrally in the subcostal field. The *sahlbergi* specimen (Fig. 22) is the darkest form of this species seen by me. It is labelled *sahlbergi* v. *obscurior* Reuter (ZMH, unpublished varietal name). The exocorium is

black save for the strongly reduced subapical spots, among which the costal spot is barely visible.

In sum, contrary to what might be suggested from the illustrations in Cobben (1960), the hemelytral colour pattern of *S. henschii* is clearly not simply a more or less direct continuation of the darkening eunomic series of *sahlbergi*.

Geographic distribution

The geographic distributions of *S. sahlbergi* and *S. henschii* are summarized below (see also maps, Figs 33, 34). New records from a country or major



Figs 20–31. *Salda*, details. — 20–25. Eumorphies of hemelytral pigmentation. — 26–27. Male parandria, posterior view. — 28–29. Right male paramere, anterior view. — 30–31. Right female 2nd gonapophysis, lateral view. — 20–22, 26, 28, 31. *S. sahlbergi* Reuter. — 23–25, 27, 29, 30. *S. henschii* (Reuter). RS = radial spot. Scale lines: a 1 mm (20–25), b 0.1 mm (26–29), and c 0.15 mm (30–31).

20–25. Mönster i framvingens pigmentering. — 26–27. Hanens parandria, bakifrån. — 28–29. Hanens högra paramer, framifrån. — 30–31. Honans högra andra gonapofys, från sidan.

biogeographic or administrative region are marked by an asterisk. More detailed collecting data are only given for the new records of *henschii* from northern Europe. With some exceptions, the records for *sahlbergi* are condensed to indicate administrative regions or provinces within a country, with more precise localities given within parenthesis.

Salda henschii (Reuter)

Acanthia henschii Reuter, 1891: 23.
Saldula umbrata Schmidt, 1937: 44.

Sweden*: Blekinge, Store Mosse, 8.vii.1954, 1 ♀, N. Gyllensvärd (EML) (Gyllensvärd 1972, as *Salda sahl-*

bergi); Bohuslän, Grinneröd, Grinneredsjön, 2.vii. 1946, 1 ♂, B. Tjeder (EML) (Tjeder 1948, as *Saldula sahlbergi*); Uppland, Runmarö, 1903, 4 ♂, 3 ♀; 1906, 1 ♂, C. Hoffstein (NRS) (Hoberlandt 1977, as *Salda sahlbergi*); Vaddö, Fjällboträsk, 7.vii. 1975, 1 ♀, P. Lindskog (NRS).

U.S.S.R.*: Leningradskaya oblast, Island of Hogland [=Sur Sari], Gulf of Finland, probably 1932, 1 ♀, W. Hellén (ZMH). Germany, Poland, Czechoslovakia, Austria, Switzerland (see Hoberlandt 1977, Péricart 1990).

Salda sahlbergi Reuter

Salda sahlbergi Reuter, 1875: 330.

Sweden: Västmanland (Linde, Grossmoßen); Hälsingland (Ovanåker); Jämtland (Bleksjön); Åsele lappmark

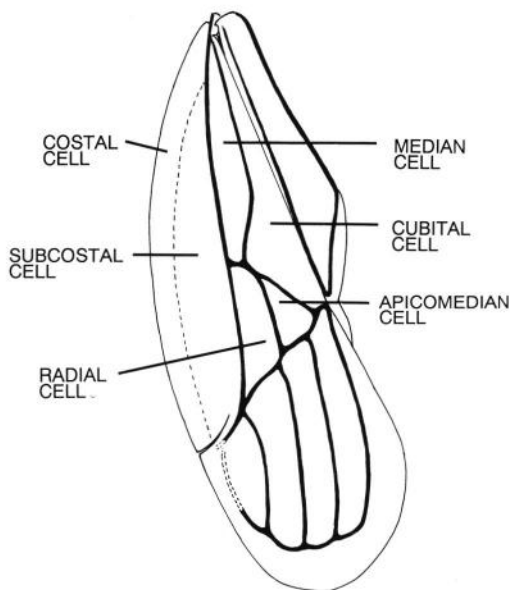


Fig. 32. Hemelytral venation and nomenclature of corial cells in Saldinae.

Framvingens ribbnät hos Saldinae, med namn på coriums celler.

(Vilhelmina); Lycksele lappmark (Galgatmyren); Pite lappmark (Arvidsjaur); Lule lappmark (Tjåmotis; Mudus) (EML, NRS). **Norway:** Eastern Buskeryd (Krok-skogen) (ZMO) Warloe 1925). **Finland:** Varsinais-Suomi (Karislojo); South Häme (Jämsä); Inari Lapland (Inari; Lutto R.). **U.S.S.R:** Leningradskaya oblast [Kexholm (now Priozersk) = the type locality]; Karel'skaya A.S.S.R [Jaakima(-vaara) (near present Lakhdenpohk'y-a)]; Kirjavalhti (near present Khelyulya) (ZMH, NRS, WAG; see also Sahlberg 1920, Hoberlandt 1977); Altayskiy kray* (Kosh-Agach) (ZIL); Chitinskaya oblast (Sretensk) (Hoberlandt 1977); Againskiy Buryat Nats. Okr.* (Ara-Ilya) (ZIL); Amurskaya oblast (Klimoutchi, 40 km W Svobodnyj) (Hoberlandt 1977); Sakhalinskaya oblast (Sakhalin, Nakashisuka) (WAG; also Hoberlandt 1971); Magadanskaya oblast (Vinokurov 1988). **Mongolia:** Ubsu-Nur aimak (near somon Barun-Turun) (Hoberlandt 1971); Central aimak (20 km S Ulan-Bator); Eastern aimak (45 km SW Bayan-Dun) (Vinokurov 1979). **China:** Heilongjiang Province (Mohe) (NUT) (Chen and Zheng 1987). **Canada*:** Newfoundland, Badger (coll.loc. 259), 24.vi. 1951, 1♀, C.H. Lindroth; Twillingate (coll loc. 276), 5.vii. 1951, 1♀, idem (ZMH).

Note: The specimens recently recorded from China (6♂3♀, 9.vii. 1984, P. Chen leg.) have been examined by me. The specimens recorded from Canada, representing the only known finds of *S. sahlbergi* in the New World so far, were originally identified as *Saldula laticollis* (Reuter) (= *Saldula fernaldi* Drake) by Carl J.

Drake and are published as that species in Lindberg (1958). They were later studied by Cobben who recognized their identity with *S. sahlbergi*. I am grateful to the late Dr Cobben who kindly brought this situation to my attention (in litt.). I have examined the two females available and find that they quite agree with typical *sahlbergi*.

Habitat

S. sahlbergi has been collected on bare boggy soils on plain bogs and small quagmires and among *Sphagnum* cushions near pools and lakes in Finland and Ladogan Karelia (Sahlberg 1920). The single specimen of *sahlbergi* I have collected originates from a raised peat-bog on bare and wet, spongy soil in a turf pit (S:Vs, Grossmossen). The specimens from Newfoundland were collected on a *Sphagnum* bog and on the bank of a pond on a quagmire (Lindberg 1958, as *Saldula fernaldi*). Published collecting data on *S. henschii* from Central Europe suggest habitat preferences closely akin to *sahlbergi* (Wróblewski 1966, Heiss 1972, as *sahlbergi*, Hoberlandt 1977). My own field experience with these species, though quite limited, well agrees with this conclusion. I collected *henschii* in Sweden on an eutrophic quagmire on a patch of bare, wet soil (Up:Väddö), and in Austria (Nordtirol: Wildmoosalm; also Heiss 1972) at the margin of a pond with wet mosses and low sedges strongly yielding under the feet.

In sum, both *sahlbergi* and *henschii* seem to be specialized inhabitants of very wet and exposed, quaggy patches of boggy soils and are apparently quite confined to fresh water environments. They are only known to appear in macropterous morphs. *S. henschii*, which has been observed in some detail by me in the field and laboratory, is a highly agile species readily performing the kind of combined jumps and short, swift flights, typical of the family. These two species therein depart also in ecological and behavioural attributes from typical (true) *Salda* species that may occur in the same major habitat [e.g. *S. morio* (Zetterstedt) and *S. muelleri* (Gmelin)]. Excepting the Nearctic monomorphic macropterous *S. lugubris* (Say) and the allied *S. alta* Polhemus, species of *Salda* mainly appear in shortwinged, flightless morphs (semibrachypterous of Cobben 1960) and are generally occupying microhabitats of a more closed structure, being found at the bases of dense and tall



Fig. 33. Distributions of *Salda sahlbergi* Reuter (triangles) and *S. henschii* (Reuter) (dots) in Europe. Distribution of *S. henschii* in Central Europe according to maps in Hoberlandt (1977) and Péricart (1990). L denotes line indicating border between Boreal and Boreo-nemoral zones (according to Sjörs 1963).

Utbredning i Europa av *Salda sahlbergi* (trianglar) och *S. henschii* (prickar). Gränslinje mellan boreala och boreo-nemorala zonerna markerad med L.

Carex-stands, amongst mosses, amidst littoral refuse, etc.

Life cycles

Adults of *S. henschii* have been collected in Central Europe from early June until late August, with

one record from early October (Schmidt 1938, Smrezynski 1954, Wróblewski 1966, Heiss 1972, Hoberlandt 1977). The earliest find of the year dates from June 1 [Poland: Upper Silesia, Tarnowskie Gory (near Katowice), a non-montane site], the latest from October 4 (Austria: Nordtirol, Wildmoosalm, a montane site, 1 300m). According to Heiss (1972) such late finds would indicate

an overwintering in the adult stage. This assumption is contradicted by other data. From 9 females of *S. henschii*, reared from larvae (L5) collected by me at Wildmoosalm (1.vii.1973, together with a few teneral adults), and kept with males in rearing jars at 18–23°C and a long-day photoperiod of ca 18 hrs light:6 hrs dark, a total of 392 fertilized eggs were obtained (deposited and kept in moist filter paper). After storage at room temperature for 1.5–2 months, 391 eggs were found to be in diapause with the development of the embryo arrested at about the same stage as described for *S. littoralis* (L.) by Cobben (1968); one egg hatched ca 30 days after deposition.

These laboratory data combined with adult phenology show that *S. henschii* hibernates in the egg stage (embryonic diapause) and has a univoltine cycle. In these respects it fully agrees with other species of the *Salda* group studied by me in more detail in the field and laboratory [*S. littoralis*, *S. muelleri*, *S. morio*, *Teloleuca pellucens*, *T. bifasciata* (Thomson)]. Further, the virtual restriction of finds of adults of *S. sahlbergi* and the remaining Old World species of the group to the period (late May–) June–August, indicate that wintering in the egg stage and univoltinism are common features of these taxa (see also Wróblewski 1966). The same situation evidently obtains for the Nearctic species as well (Polhemus & Chapman 1979, Polhemus 1985) (excepting an apparent regional bivoltinism in *S. lugubris*). Rare odd records of larvae or adults from the late part of the season in species of this group, rather than representing a true facultative second generation, are more likely to result from occasional eggs of weaker diapause intensity, as the single hatched egg in the laboratory sample of *S. henschii* above. A partial exception to this pattern seems to be provided only by some regional populations of *S. littoralis*, the most widely distributed species of the group, known to have a strongly manifested (“obligate”) embryonic diapause in populations from northern as well as southern Europe (Jordan & Wendt 1938, Cobben 1968, 1985, Lindskog unpubl.) However, in some areas along the Atlantic coasts of NW Europe (SW Norway, ? the British Isles) and on Iceland a wintering also in the adult stage seems to occur. This is strongly suggested by adults collected in April (incl. first week) in these areas seen by me in collections or reported in the literature (Fristrup 1945). This may be compared to populations from South and Central Sweden (Baltic

coastal region) invariably hibernating as eggs, where the first adults of the year hatch during the first decade of June, more exceptionally (unusually warm and sunny springs) during the last week of May (Lindskog unpubl.).

Biogeography

Zonal-ecological relationships

The known localities of *S. sahlbergi* and its apparent sister species, *S. henschii*, are mapped in Figs 33, 34. Several interesting patterns emerge here inviting comments and tentative explanations.

The Fennoscandian localities of *henschii* are fairly isolated and disjunctively separated from its occurrences in montane and perimontane areas in Central Europe (Fig. 33). An outlier in the Harz Mts (Germany) represents the single occurrence located most proximate to the Fennoscandian sites. The northern limit of *henschii* in Fennoscandia approximates the southern limit of the distribution of *sahlbergi* in this area, i.e. around Lat. 60°N. This essentially corresponds to the boundary or transition area between the Euboreal and Subboreal zones in this particular region (as defined by Emelyanov 1974), i.e. the Northern Coniferous (Taiga) and the Mixed Forest zones, or—following the more elaborate division employed by Nordic geobotanists—the boundary between the southern Boreal sub-zone and the Boreo-nemoral (Hemiboreal) zone (Sjörs 1963, Ahti et al. 1968). As indicated in Fig. 33, the southernmost localities of *sahlbergi* are quite neatly aligned along the course of this border, known by Nordic plant geographers as the “*limes norrlandicus*”. Further, especially noteworthy is the fact that the few records of *henschii* from northern Europe all refer to fresh water wetlands situated in lowland coastal areas (The Baltic and the North Sea), including an outlying insular occurrence in the Gulf of Finland. This evident restriction of *henschii* to coastal lowlands in the north might seem unexpected when considering the ecological settings occupied by the species in Central Europe. Here its distribution is centered to the montane coniferous belts. Accordingly, in the Northeastern Alps region the main distributional focus of *henschii* is at altitudes around 1 300 m, with an isolated occurrence recorded at 2 100 m, i.e. somewhat above the timber-line (Heiss 1972).

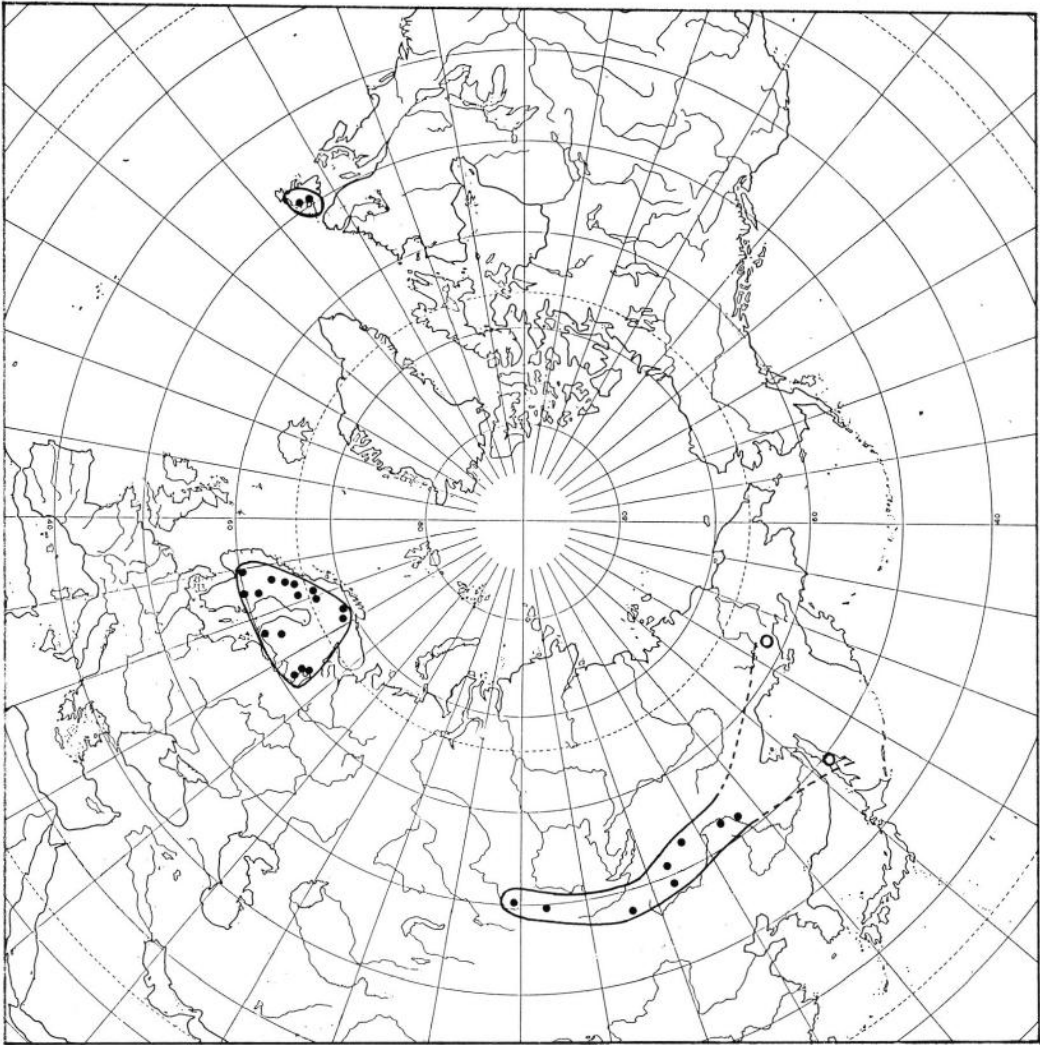


Fig. 34. World distribution of *Salda sahlbergi* Reuter. Open dots mark records without information on exact location. Världsutbredning för *Salda sahlbergi*.

In a comparative perspective, the Fennoscandian-coastal/Central European-montane range disjunction in *S. henschii* partly matches a special kind of distribution pattern observed in various boreal and boreo-montane (or boreo-alpine) insects. The northern range is here typically splitted into two main centers: (1) the Scandinavian mountains and the Coniferous zone of northern Fennoscandia, and (2) the coastal areas and archipelagos of western Sweden, and, notably, the Baltic coast

of southern Sweden and Finland. The distribution of *S. henschii* might be likened to and discussed with reference to that particular pattern, though differing of course in one principal respect; i.e. the northern subrange of this species does not include the Boreal zone proper. Instead, it is here represented by its sister species, *S. sahlbergi*, which thus stands out as a vicariant, true boreal species. The present distribution pattern has been primarily documented and studied in more detail

in certain species of aquatic Coleoptera (Dytiscidae) and Heteroptera (Corixidae). Here the more or less isolated coastal populations are restricted to rock-pool habitats (Lindberg 1944:156 ff, Jansson 1980). According to the customary interpretation of this pattern, the coastal areas would presently serve as a kind of extrazonal refugia for these species. Populations once occurring in the present interior parts of southern Finland and Sweden in Late Glacial and early Postglacial times subsequently got extinct here with the progressive amelioration of the climate and the disappearance of suitable habitats (early successional ponds and pools). However, as a result of the continuing isostatic land uplift of this formerly heavily glaciated region, new suitable habitats are successively created with the emergence of new land along the coastal fringes that allows for the persistence here of these species, well remote from their present main northern, respectively mid-latitude montane centers of occurrence (see further Jansson 1980, for a detailed account).

Various combinations of climatic and edaphic conditions peculiar to the Baltic coastal regions, including the pervasive role of the secular land uplift, have been invoked to account for the extrazonal occurrence here of a number of boreo-arctic, boreo-alpine/montane, as well as basically continental, stepicolous plants and insects (cf. above and e.g. Nordman 1928, Brinck 1966, Mikkola et al. 1987). We may then ask whether a similar relictual or "pseudorelictual" (cf. Lindroth, 1949:677 ff) character also might be construed for the apparent confinement of *S. henschii* to coastal areas in Fennoscandia, as opposed to mountains in the south. Any special properties of its preferred habitats that would explain this pattern do not readily come to eye. As summarized above, this shore bug is only known to inhabit certain kinds of fresh water wetlands representing later and fairly stable stages of the hygric successions. Seemingly suitable habitats of that kind are common in coastal as well as inland areas of this region. It is true, however, that the bog formations within the present coastal lowland fringes of Fennoscandia are of an averagely younger age; i.e. they have developed more recently in place of former bays and straits, which have been successively cut off from the adjacent sea as a result of the land uplift (amounting presently to ca 50 cm/100 yrs at the Baltic coast of Sweden around Lat. 60°N) and become transformed to fresh water habitats. Com-

bined with a geographically marginal location, this situation might render the coastal-near wetlands the quality of more young pioneer habitats with less full and stable species complements if compared with their inland counterparts. If so, we may speculate that the restriction of *S. henschii* to coastal regions in Fennoscandia might be due to a relaxation here of a "diffuse competition" and other interactions with the present "true" zonal biota of this major region, which are preventing its establishment in more inland core areas. Needless to say, in the absence of more detailed data such an "explanation" must remain purely conjectural. In fact, one may seriously question whether present ecological theory actually is capable of identifying the relevant data for testing such a hypothesis. The aim of the present discussion is simply to focus on the importance of selecting a proper temporal scale for causal interpretations of distribution patterns. While being part-and-parcel of paleobiology and historical biogeography, the recognition that the distribution and abundance of organisms may be related to factors varying over very different spatio-temporal scales is only recently gaining some foothold among ecologists (see Hengeveld 1987, 1988). The isostatic land uplift of formerly glaciated regions therein serves as a particularly instructive example of a long term process that may ultimately trigger the distribution patterns of various organisms occurring there. Accordingly, we might hypothesize that the localities of *S. henschii* in Fennoscandia point at those areas where a successional decline in habitat suitability and local extinctions of the species have been counterbalanced into recent times by the creation of new suitable habitats at a sufficient rate and spatial scale, a secular process strongly affected by the regional land uplift.

Whatever the true ecological and Holocene historical background of the distribution of *S. henschii* in Fennoscandia may be, the few available records most certainly reflect the true rarity and restricted occurrence of the species here rather than merely insufficient collecting. The single and seemingly quite isolated find from the Eastern Baltic region, on the Island of Hogland, merits some special attention in terms of the present discussion. This small island (length 11 km, max width 3 km), situated in the Gulf of Finland at a distance of 43 and 55 km from the mainlands of Finland and Estonia respectively, consists of an crystalline outcrop and attains a maximum height

of 158 m a.s.l. There are a few small lakes, otherwise bogs and marshes are lacking. The coasts are steep, rocky or stony. Due to its height this island has never been completely inundated during post-glacial times (data from Lindroth 1949:263 ff). The find of *henschii* was evidently made by W. Hellén during his collecting trip to this and other islands in the Gulf of Finland in 1932. In reporting on his more remarkable finds of Heteroptera from these localities (Hellén 1934), *S. henschii* (or *sahlbergi*) is not mentioned (evidently mistaken for some more common species). One might guess that the *henschii* specimen was collected on the quagmire at the Lake Veteljärvi where the saldid *Micracanthia fennica* (Reuter) was collected 3.vii.1932 (Hellén 1934:19). Thus, other finds of *S. henschii* and *S. sahlbergi* have regularly been made in boggy habitats characterized by the presence of either *M. fennica* or the related *M. marginalis* (Fallén), both species having exacting ecological demands and more or less localized occurrences in Fennoscandia. An interesting analogue to *S. henschii* is provided by the ground-beetle, *Carabus problematicus* Herbst, which appears with different subspecies in boreo-arctic and montane regions of Europe. Like *S. henschii* the singular locality of this species within the entire Eastern Baltic region is on Hogland (Lindroth 1945, 1968). Lindroth (1949:267) suggested that the occurrences on Hogland of this and some additional boreo-montane carabids (e.g. *Bembidion schuettepeli* Dejean), the latter also occurring on the adjacent coastal-near mainlands, are relics from early postglacial stocks in this area. He believed that their presence on Hogland may be of quite an old date, considering that the island has remained emergent throughout the Postglacial.

Present records of *S. sahlbergi* (Fig. 34) suggest a markedly discontinuous Holarctic-boreal distribution comprising three main subranges: (1) Fennoscandia, (2) a relatively narrow belt around Lat. 50°N extending from Siberian Altay over Trans-Baikalia and Northern Mongolia to the Far East, and (3) Eastern North America (Newfoundland). Though similar NW European/ C Siberian range disjunctions by no means are rare among the boreal biota (e.g. Varga 1977), localities of *sahlbergi* may conceivably exist within the northern stretches of the European U.S.S.R. between Lake Ladoga and the Urals, an entomologically poorly investigated area, that would partly fill this distributional gap. The lack of records from the West

Siberian Lowlands might point at an actual absence of the species rather than being due to insufficient sampling, considering that a similar West Siberian interruption is a recurrent component of the distribution patterns of many boreal and temperate insects and other organisms with diverse zonal-ecological affinities (see further below). The New World records from Newfoundland suggest that *S. sahlbergi* may be more widely distributed in the Canadian and Alaskan northlands whose saldid fauna is still imperfectly known.

Vicariance patterns

The type of vicariance pattern shown by the present two species, where one species occupies a Holarctic-boreal range (*S. sahlbergi*) and its sister species being a European endemic (*S. henschii*), is duplicated by other putative pairs of sister species among cold adapted Saldidae. Suffice it here to mention one example from the *Salda* group. Thus, *Teloleuca bifasciata* is a Holarctic-boreal species, in Europe (Fennoscandia and eastwards) confined to the northernmost subarctic-subalpine regions. Its sister species, *T. brancziki* (Reuter), is restricted to the Carpathian and Caucasus Mts of SE Europe. [Their status as sister species is supported by shared derived features of the male genitalia and colour patterns of the hemelytra and other body parts (Lindskog in prep.).] The sister species of *bifasciata* + *brancziki* is evidently *T. kuznezovi* Lindberg, endemic to Far East Asia (for the distribution of *Teloleuca* spp., see Cobben 1985: map 4).

Any closer analysis of the historical biogeographic meaning of the present vicariance pattern falls outside the scope of this paper. It requires further studies of phylogenetic relationships within the *Salda* group and will better be performed within the context of a more comprehensive biogeographic study of the Holarctic Saldidae (Lindskog in prep.). I will only make a few points and suggestions here. By necessity, these will essentially take the form of assertive statements, of heuristic value at best, awaiting support from more detailed data and arguments.

Basically, the vicariance pattern displayed by *S. sahlbergi/henschii* brings forward some issues centered on the nature and historical interactions of two major areas of endemism recognized in Eurasia (or in Holarctic biogeography): Europe and Angara. Among the plethora of "zoogeogra-

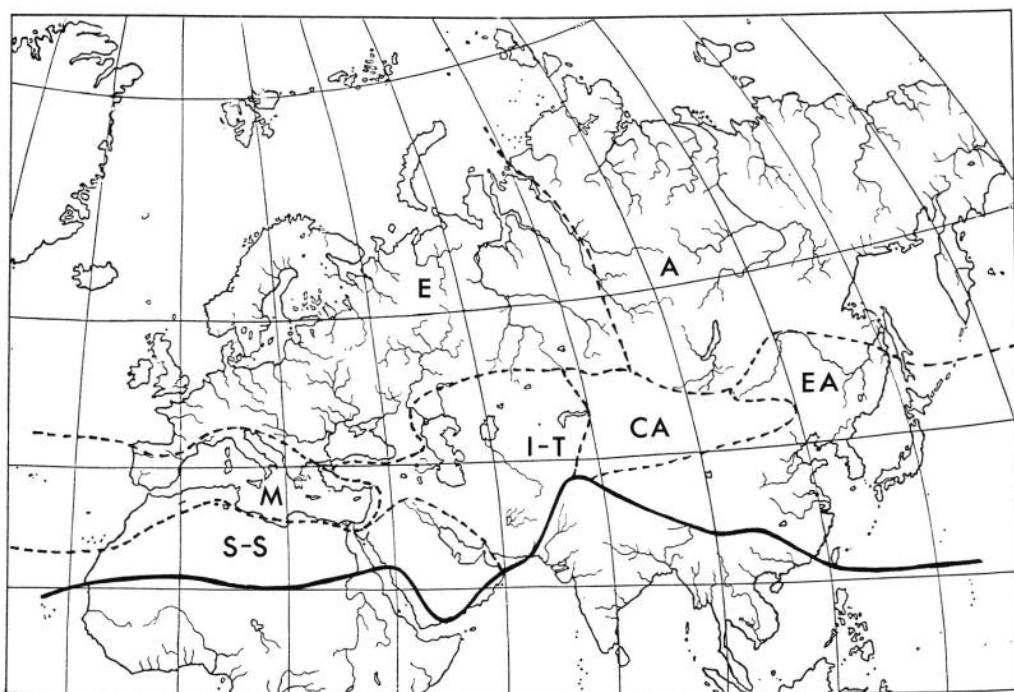


Fig. 35. Division of the Palearctic into zoogeographic subregions: (E) European, (A) Angara, (M) Mediterranean, (S-S) Saharo-Sind, (I-T) Irano-Turanian, (CA) Central Asian, and (EA) East Asian. After Vtorov & Drozdov (1978) (redrawn from Beschovski 1984).

Zoogeografiska underregioner i Palaearktis.

phical" regionalizations of Eurasia proposed in the literature, the subdivisions of the Palearctic outlined by Vtorov & Drozdov (1978) (as reproduced in Beschovski 1984:fig. 1) is chosen here as basis for the following discussion. These subregions (Fig. 35) are roughly comparable to a number of major areas of endemism that are more generally agreed upon and supported in the literature.

According to an old standard concept in Holarctic biogeography, a majority of the species groups of insects and other organisms inhabiting the present boreoarctic and boreomontane regions of the Old and New World ultimately derive their origin from "Angaran" ancestors (or, alternatively stated, "Siberian" or "Asian" ancestors) (e.g. Kolbe 1913, Uvarov 1929, Van Dyke 1930, Kusnezov 1935, Reinig 1937, etc). Critical phylogenetic (cladistic) biogeographic analyses of this relationship are still largely wanting and much needed. However, this particular inference may seem to be amply supported by a variety of comparative

biological and distributional data, and, not the least, by paleogeographical and paleoenvironmental considerations. The ancient Angaridan part of Asia, with its vast expanses of land of long geological continuity and great physiographic diversity with old mountain systems, and encompassing the geographic center of the Neogene cooling of the Laurasian realm, is readily recognized as a major arena for the evolution, diversification, and successive expansions of cold-adapted biota into more peripheral, appendant areas as Europe.

The now well documented alterations of species ranges during the Pleistocene, including extinctions on continental scales (e.g. Matthews 1977, Coope 1979, Hammond et al. 1979), clearly complicate the use of extant distributions as data for historic biogeographical reconstructions. According to a leading paleoentomologist (Coope 1979), present distributions of species only reflect the current distributions of their preferred environments, therein decrying any attempts at deeper

historical inferences from such data. Such a view depreciates or ignores the potential role of phylogenetic (cladistic) biogeographic analysis as a mean of retrieving the more original distribution patterns (initial endemic affiliation) of species, also where the original ranges may have become more or less altered and obscured by subsequent dispersal and/or extinctions. The strength of the cladistic approach in the context of Holarctic biogeography is nicely demonstrated by Tangelder (1988) at her attempts to reconstruct original distribution patterns and their historical roots in a group of crane flies (Tipulidae).

Phylogenetic-biogeographic patterns within several groups of northern cold-adapted Saldidae (*Chiloxanthus*, "*Saldula*" *orthochila* species group) were discussed by Lindskog (1980). I concluded that these patterns have their origins in Neogene (primarily Miocene) events and, further, that original areas of endemism may be separated from some more recent Pleistocene and Holocene modifications of species ranges. Similar results were reached by Tangelder (1988) in a much more detailed and complete study of tipulid flies. These general conclusions are in line with the concept, supported by recent studies of insect fossils, that the evolutionary origins of the diversity and biological characteristics of the insect fauna of Holarctica are closely mated to Tertiary geological and paleoclimatic events (cf. Matthews 1979, 1980). There is no fossil evidence for any speciation events in insects during the Pleistocene (Coope 1978, 1979). Further, in those instances where a more complete resolution of the cladistic relationships within these and other Holarctic-boreal insect taxa has been accomplished, the groups appear to be primitively anchored in Asia.

Turning to *S. sahlbergi* and *S. henschii*, the present insufficient knowledge of their relationships to other ingroup taxa (cf. above) precludes any direct inferences on the distribution of their common ancestor. However, by analogy with some cladistically better resolved groups and in considering the vicariance situation of these two species as belonging to a generalized pattern with a common historical background, I suggest the following scenario to account for their distribution. Accordingly, assume for the sake of argument an Angaran origin of the *sahlbergi* group (with areas of origins of species and groups as defined by Brundin 1981). The incipient ancestor of *sahlbergi* + *henschii* is hypothesized to have

dispersed into Western Siberia and Europe at some time in the Late Miocene-Pliocene concomitant to the progressive expansion of cool-temperate and, later, boreal landscape formations from the northeastern highland and mountainous regions of Asia towards the west and southwest (cf. Sinitsyn 1965, Axelrod 1975, Pearson 1978). The continuity of the more western and eastern populations was later severed. This isolation is likely to have been effected by the spread of steppe formations at mid latitudes in the interior part of the continent and, further, from expansions of forest-tundras and tundras at higher latitudes concomitant to an accelerating climatic cooling culminating with the freezing of the Arctic Basin and the first continental glaciations in Mid and Late Pliocene (cf. Matthews 1979). Environmental alterations (aridification) affecting the southern parts of the West Siberian Lowlands between the Altay-Sayan and the Ural Mountains are suggested to have acted as primary isolating agents. The western segregate evolved into *S. henschii*, the eastern into *S. sahlbergi*, a more cold-adapted species.

According to the scenario above, *henschii* is interpreted as a European endemic, originally related to *sahlbergi* by a west/east vicariance pattern, not a "boreo-montane(-alpine)" pattern as might be suggested from their recent distributions. The original ranges must have been considerably modified by Pleistocene climatic events. Most importantly, *S. sahlbergi*, here interpreted as a primitively Angaran species, has invaded the European area to attain a "Euro-Siberian" distribution. Similarly, an expansion into North America via Beringia is assumed. The time for the first arrival of the species in Europe is of course unclear. Species of Coleoptera presently confined to Eastern Siberia appeared in Western Europe during spells of cold, continental climate during the Middle Last Glaciation (Angus 1973, Coope 1979). Such periodic extensions of continental Asiatic species into Europe should have taken place repeatedly during the Pleistocene. Some of these contracted to eastern Eurasia during the last maximum ice advance, while some may also have found refugia in Europe. Other species have appeared in Europe during Late Glacial and Early Postglacial times.

The present discussion focuses the attention on various issues centered on what is known in the zoogeographic literature as the "Yenisey faunal divide" (Johansen 1955) or the "Johansen-line" (de Lattin 1967). This corresponds to what is de-

picted in Fig. 35 as the border between the European and Angaran areas of endemism (subregions). It corresponds to the boundary between the West Siberian Lowlands and East Siberian highlands and, concurrently, the transitional zone between an Atlantic respectively Pacific influence on the climate (Johansen 1955, Emelyanov 1974). Paleogeographically this corresponds to the western rim of the Siberian plateau (Angarida) that was separated from Europe (Fenno-Sarmatia) during the Paleogene by the epicontinental sea (Obik Sea and Turgai strait) then covering the present West Siberian Lowlands and connecting the Arctic Ocean with the Tethys Sea in the south. Also after the withdrawal of this sea the West Siberian lowland must have continued to act as a major ecological discontinuity and biogeographic barrier by its character of an immense plain largely dominated by wetlands that separate more elevated and mountainous regions to the west and east.

Distributional and systematic data on a multitude of insects and other organisms evidence the role of the West Siberian Lowlands as the major biogeographic divide in Northern Palearctic. This concerns vicariance situations between West and East Eurasia of sister taxa of different taxonomical rank, as well as disjunctive distributions within species. The latter pattern characteristically involves a break in the distribution of boreal species somewhere between western Europe and the Ural Mts in the west and the Yenisey Valley and the Altay-Sayan Mts in the east. This "West Siberian interruption" (cf. Kusnezov 1935) is documented in many insect groups of the Eurasian Arboreal (e.g. Lindskog 1980, Beschovski 1984, Tangelder 1988). Examples of this pattern in the Saldidae include *Saldula orthochila* (Fieber), *S. nobilis* (Reuter) (discussed and mapped by Lindskog 1980), and *Teloleuca pellucens* (cf. Cobben 1985:map 4). As noted above, also *S. sahlbergi* may be referred to this distributional pattern (Fig. 34). In the case of the latter and other species associated with boreal bog habitats, their apparent absence from the West Siberian Lowlands, qualifying as "the Largest Bog Region of the Earth" (Walter 1979:242 ff), may seem somewhat paradoxical and rather suggesting incomplete sampling. However, their absence from this area dominated by monotonous expanses of string bogs and bog lakes may well be real. It may conceivably be related to adverse environmental effects imposed by the very special hydrological

conditions of the Ob-Irtysh Basin. These promote extreme summer floods of the low watersheds (with rivers running up to 12 m above low water) and the formation of vast expanses of water through their coalescence with bog lakes (cf. Walter, op.cit.). This creates a highly unstable and hazardous environment that may be mastered by relatively few species only.

In conclusion, the capacity of the West Siberian Lowlands to function as barrier separating European and Angaran faunas has been subject to recurrent breaks through geological time. Climatic variations from late Tertiary onwards influencing the environmental settings of the southern parts of the West Siberian Lowlands and the the adjoining hilly country of Northern Kazakhstan, presently occupied by forest steppes and steppes, are likely to have been significant in promoting episodes of faunal exchanges. Accordingly, during periods of cooler and more humid climates these areas may have provided transient pathways for a dispersal of elements of the Eurasian Arboreal.

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Sammanfattning

Salda henschii (Reuter), tidigare känd från Melaneuropas bergstrakter och ofta felaktigt sammanförd med *S. sahlbergi* Reuter, anmäls från Sverige och från den sovjetiska ön Hogland i Finska viken. Tidigare fynduppgifter om *S. sahlbergi* från Blekinge, Bohuslän och Uppland avser samtliga *S. henschii*. Karaktärer ges för åtskiljandet av dessa båda arter, och deras nuvarande placering i släktet *Salda* ifrågasätts. *S. sahlbergi* rapporteras för första gången från Nordamerika (Newfoundland). De båda arternas habitatval och livscyklar redovisas och diskuteras. Arternas utbredningar revideras och ägnas en biogeografisk analys med tonvikt på vikariansförhållanden och historiskt betingade ekologiska fenomen.